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# Modelling habitat selection and distribution of the critically endangered Jerdon's courser *Rhinoptilus bitorquatus* in scrub jungle: an application of a new tracking method

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**Summary**

**1.** Jerdon's courser *Rhinoptilus bitorquatus* is a nocturnally active cursorial bird that is only known to occur in a small area of scrub jungle in Andhra Pradesh, India, and is listed as critically endangered by the IUCN. Information on its habitat requirements is needed urgently to underpin conservation measures. We quantified the habitat features that correlated with the use of different areas of scrub jungle by Jerdon's coursers, and developed a model to map potentially suitable habitat over large areas from satellite imagery and facilitate the design of surveys of Jerdon's courser distribution.

**2.** We used 11 arrays of 5-m long tracking strips consisting of smoothed fine soil to detect the footprints of Jerdon's coursers, and measured tracking rates (tracking events per strip night). We counted the number of bushes and trees, and described other attributes of vegetation and substrate in a 10-m square plot centred on each strip. We obtained reflectance data from Landsat 7 satellite imagery for the pixel within which each strip lay.

**3.** We used logistic regression models to describe the relationship between tracking rate by Jerdon's coursers and characteristics of the habitat around the strips, using ground-based survey data and satellite imagery.

**4.** Jerdon's coursers were most likely to occur where the density of large (> 2 m tall) bushes was in the range 300–700 $ha^{-1}$ and where the density of smaller bushes was less than 1000 $ha^{-1}$. This habitat was detectable using satellite imagery.

**5.** *Synthesis and applications*. The occurrence of Jerdon's courser is strongly correlated with the density of bushes and trees, and is in turn affected by grazing with domestic livestock, woodcutting and mechanical clearance of bushes to create pasture, orchards and farmland. It is likely that there is an optimal level of grazing and woodcutting that would maintain or create suitable conditions for the species. Knowledge of the species' distribution is incomplete and there is considerable pressure from human use of apparently suitable habitats. Hence, distribution mapping is a high conservation priority. A two-step procedure is proposed, involving the use of ground surveys of bush density to calibrate satellite image-based mapping of potential habitat. These maps could then be used to select priority areas for Jerdon's courser surveys. The use of tracking strips to study habitat selection and distribution has potential in studies of other scarce and secretive species.

*Key-words*: Andhra Pradesh, India, logistic regression, satellite imagery, species–habitat model, tracking strips

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## Introduction

Jerdon's courser *Rhinoptilus bitorquatus* (Blyth) (Charadriiformes: Glareolidae) is a nocturnal cursorial bird that was first described in the 19th century and not reliably recorded after 1900 until its rediscovery in 1986 (Bhushan 1986). Since then, it has only been seen in a few restricted areas of scrub jungle near Cuddapah in Andhra Pradesh, India. In the 19th century the species was also recorded from several other locations including the Godaveri valley, up to 600 km away. It might still occur there and in similar habitat elsewhere (BirdLife International 2001).

Jerdon's courser is categorized as critically endangered in the International Union for the Conservation of Nature (IUCN) Red List (Hilton-Taylor 2000) because it is believed to have a small and declining population. Information on its distribution, population and habitat requirements is sparse (BirdLife International 2001) because Jerdon's coursers are difficult to study. They are active nocturnally and the wooded nature of their habitat, together with their retiring habits, make visual searches in daylight unproductive. Recent records of Jerdon's coursers have been obtained visually during night-time walks in lightly wooded scrub jungle in which the observer scans the ground with the aid of a torch (Bhushan 1986). This method requires several hours of searching per sighting, even in the area where sightings are most frequent. In addition, the efficiency of night-time searching is unknown and is likely to vary with habitat characteristics, such as the density of bushes and the nature of ground vegetation, so its value for assessing habitat selection is questionable.

The objectives of this study were to quantify the features of scrub jungle that correlate with the extent of its use by Jerdon's coursers and to develop a method by which potentially suitable habitat could be mapped over large areas to facilitate the planning of surveys of Jerdon's courser distribution. We used tracking strips, which retain characteristic footprints of Jerdon's courser (Jeganathan *et al*. 2002), to study the selection of habitat. We then compared statistical models of habitat selection based upon ground-based vegetation surveys and satellite imagery. We propose a two-step procedure in which ground-based vegetation surveys are used to calibrate the mapping of suitable habitat from satellite images. Such maps could be used to identify priority areas for surveys.

## Study area

The study was conducted in the Sri Lankamaleswara Wildlife Sanctuary, in the valley of the River Sagileru, Cuddapah District, Andhra Pradesh, India (14°N, 79°E), and in similar habitat just outside the reserve boundary. We studied habitat selection by Jerdon's coursers in areas of open scrub and trees in the alluvial wash below the eastern slopes of the Lankamalai hill range at altitudes of 150–300 m.a.s.l. These areas were bounded to the west by the dense scrub and forests of the higher elevations of the hills and to the east by pastures, orchards and croplands in the valley bottom (Fig. 1).

The scrub zone was traversed from west to east by streams that run in the monsoon season (May–October) and dry out during the rest of the year. Corridors of dense scrub and trees were found along the margins of these streams, with a mixture of open areas and scrub between. The substrate consisted of alluvial soil, gravel or stones. The ground vegetation was sparse and dominated by grasses, which dry up during the dry season. The area was used by people from villages in the Sagileru valley for grazing herds of domestic water buffalo *Bubalus bubalis* (L.), sheep *Ovis aries* L. and goats *Capra hircus* L. and for woodcutting. Wild large herbivorous mammals in our study sites were chinkara *Gazella bennettii* (Sykes), chital *Axis axis* (Erxleben) and black-naped hare *Lepus nigricollis* Cuvier.

## Methods

### TRACKING STRIPS

Fine soil was collected near the reserve and passed through a 1-mm sieve. A strip of ground 5 m long and 25 cm wide was scraped clear of stones and vegetation. The soil was spread along the strip, flattened into a layer 1–2 cm thick, slightly compacted and smoothed with a builder's trowel. Soil collected adjacent to the strip was dusted onto its surface with a sieve to camouflage the difference in colour that might otherwise cause birds to avoid the strip. The position of the strip was recorded using a global positioning system (GPS; Garmin GPS III).

### SELECTION OF TRACKING STRIP LOCATIONS

Strips were deployed in 2001 and 2002 in 11 blocks of scrub jungle (Fig. 1). In block H, which overlapped with the area in which Jerdon's courser has been seen repeatedly since its rediscovery in 1986, strips were placed at irregular spacing (24–72 m between nearest neighbours) in places where the density of bushes resembled that at precise locations within the block where Jerdon's coursers had been seen. Other blocks were chosen in similar open scrub habitat. Within each of these blocks, strips were placed on a square grid with 50 m (blocks A, B, C, D, J and K) or 100 m (E, F, G and I) spacing. The grids were laid out within irregularly shaped areas of apparently suitable habitat using a GPS. Each strip was placed as near as possible to the place specified by the grid, but a few strips were displaced by a few metres if the specified place coincided with a large bush or tree. Apart from these necessary displacements, strips were deployed at random with respect to habitat within all blocks but H.

### CHECKING TRACKING STRIPS FOR FOOTPRINTS

Tracking strips were usually checked at intervals of 4 days (range 1–7 days). Simulated bird footprints remained

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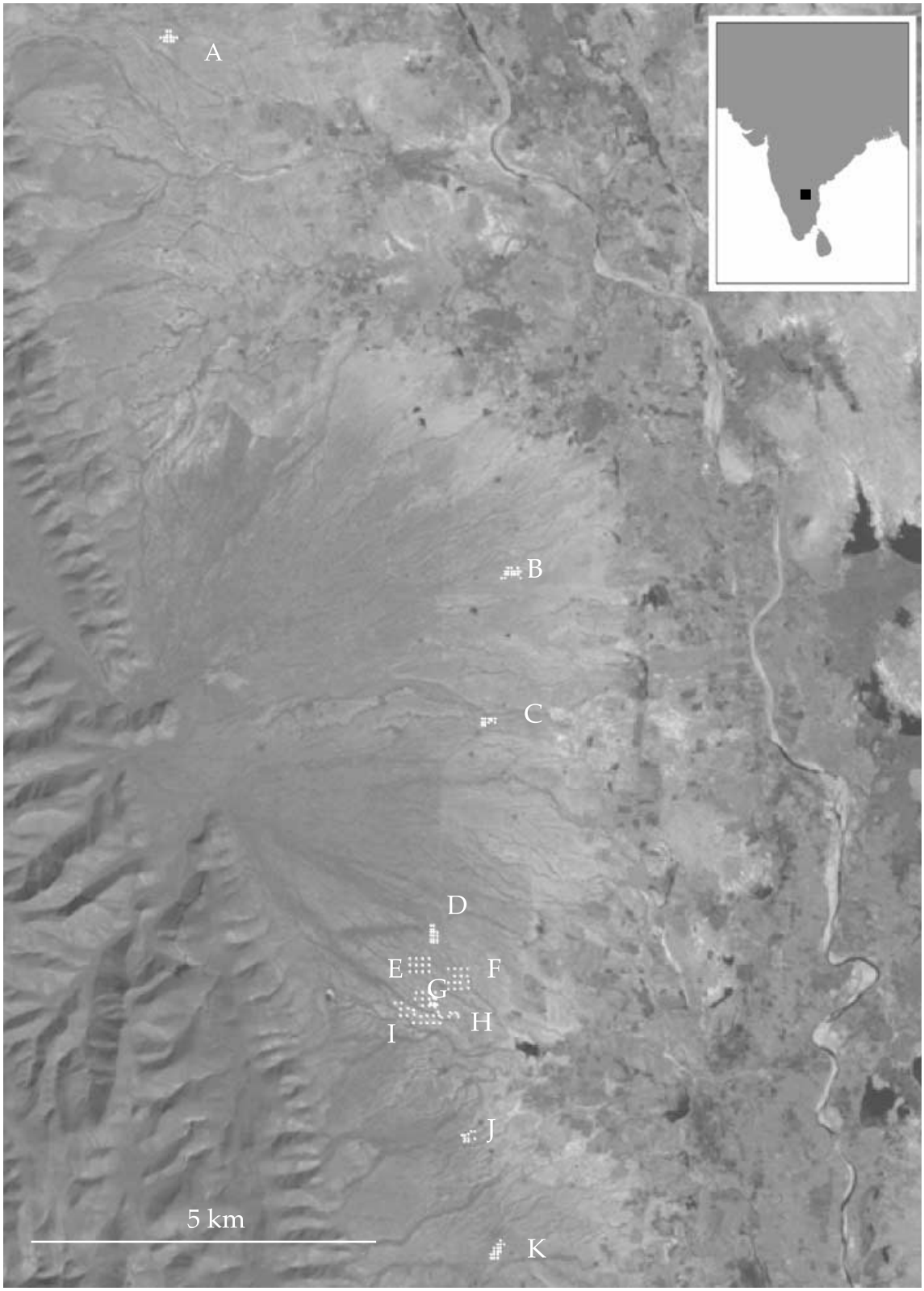


**Fig. 1.** Landsat 7 Enhanced Thematic Mapper image of the study area (path/row 143/050; panchromatic band 8) for 6 December 2000. White dots show the locations of tracking strips. Letters identify blocks as listed in Table 1. The River Sagileru with its adjacent patchwork of cultivated fields, pastures and irrigation reservoirs is visible on the eastern side and the Lankamalai Hills on the west. The filled square on the inset map shows the location of the study area within India.

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in good condition for at least 8 days provided there was no rain. Identification of Jerdon's courser footprints followed the method of Jeganathan *et al.* (2002). Confusion with other species is unlikely (see the Discussion). When Jerdon's courser footprints appeared on a strip during the interval between two checks this was treated as a single tracking event, regardless of the number of footprints or their distribution on the strip. Tracking

events were infrequent, so it can reasonably be assumed that tracks were made on just one of the nights between checks. When most of a strip had been disturbed by strong wind, rainfall, humans or livestock, the period between such a visit and the previous one was excluded from further analysis. After recording footprints, the surface of the strip was smoothed and prepared as described above. The number of nights of monitoring was calculated for each strip and averaged 32·5 nights per strip (range 3–79). Only six strips were monitored for less than 10 nights.

### RECORDING HABITAT AROUND TRACKING STRIPS

Within a 10-m square plot centred on each strip, all bushes and trees were assigned to 1-m height classes with the help of a calibrated stick, and identified to species. Specimens were taken and compared with herbarium material to confirm their identity. For analysis, we divided these counts into small (< 2 m tall) and large (> 2 m) bushes and used principal components from an analysis of the proportions of the 12 most abundant tree and bush species. The numbers of plants of *Dodonaea viscosa* Jacq. and tussocks of the grass *Cymbopogon citratus* (DC.) Stapf. in the plot were also counted as the only other large plants present. Visual estimates to the nearest 5% were made of the proportion of the substrate within the square that was soil, gravel (mean stone diameter < 2 cm) and stones (mean stone diameter > 2 cm) and the proportion of the square covered by grasses. We recorded signs of woodcutting by humans, such as recently cut branches and trunks and changes in growth form of the larger bushes and trees caused by past cutting.

### SATELLITE IMAGERY

We used a georeferenced Landsat 7 Enhanced Thematic Mapper image of the study area (path/row 143/050) for 6 December 2000. This image was selected because it was cloud-free, close in time to the study period and obtained in the dry season when there is marked contrast in the appearance on the image of bushes, which bear green leaves, and the ground layer, which is bare soil or stones and sparse grass.

Two control points were identified on the image that could be located with precision on the ground. These were the centre of a road bridge crossing the River Sagileru and the margin of a large pond within the reserve. The universal transverse mercator (UTM) coordinates of these locations on the image were compared with readings taken at the sites with a GPS, which was also used to record the locations of tracking strips. The readings for these two sites were 52 m and 57 m further south than their coordinates on the satellite image, but their west–east locations were very similar. Hence, when identifying the image pixel whose centre was closest to the location of a tracking strip, we added 54 m to the strip's south–north GPS coordinate. Although this was a crude way to match the GPS locations with satellite pixels, it was sufficiently accurate (within about 10 m) for the purpose because it was only necessary to identify the pixel within which each strip or plot lay.

We analysed reflectance values in all nine available bands (bands 1, 2, 3, 4, 5, 6·1, 6·2, 7, 8) for the pixel the centre of which was nearest to the tracking strip. Pixels were 14 $m^2$ for the panchromatic band 8, 57 $m^2$ for thermal bands 6·1 and 6·2 and 28·5 $m^2$ for the other bands.

In addition to using the reflectance values themselves, we also calculated a normalized difference vegetation index (NDVI) as:

$$\text{NDVI} = (\text{band 4} - \text{band 3})/(\text{band 4} + \text{band 3})$$

Other studies show that this index is strongly correlated with the biomass density of green vegetation in the pixel (Curran 1980).

### STATISTICAL ANALYSIS

#### *Principal components analysis of bush species composition*

We selected the 12 most abundant tree and bush species in all plots combined and expressed the number of individuals of each species in each plot as a proportion of the plot total for those species. This proportion was arcsine square root transformed and Pearson correlation coefficients calculated for each pair of species (see Appendix 1). Principal components analysis (PCA) with no rotation was performed on the matrix of correlations.

#### *Tracking rate in relation to vegetation survey and satellite image variables*

The probability per night of monitoring that a tracking strip was crossed by a Jerdon's courser was modelled by logistic regression as a function of variables measured around each strip. We used GLIM 4 to fit logistic regression models, with the number of Jerdon's courser tracking events as the dependent variable and the number of nights for which the strip was monitored as the binomial denominator (Crawley 1993). The analysis assumed that each night of monitoring was an independent binomial trial, even for different nights at the same location. Model selection was by a step-up procedure, beginning with the effects of single variables and their squares. The square of an independent variable was included in the model along with the variable itself to allow for curvilinear quadratic relationships. At each step, the change in deviance from including each of the variables not already included in the model, together with its square, was calculated and the most significant of these was selected, provided that its effect was significant at $P < 0{\cdot}05$. Interaction terms were not considered. After including a new variable, the effects of all the variables already in the model, including squares,

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was tested by deleting each in turn and performing a likelihood-ratio test. Any term whose effect was not significant at $P < 0{\cdot}05$ was deleted. The procedure ended when no significant reduction in deviance resulted from the inclusion in the model of any further terms. This resulted in the selection of a minimal adequate model (MAM; Crawley 1993) in which the deletion of any variable or factor resulted in a significant increase in the deviance, and none of the variables and factors excluded from the model had a significant effect when included. For all the MAM generated in these analyses, the residual deviance was less than the residual degrees of freedom, so no adjustment was made for overdispersion.

Our model selection procedure, as described above, did not take into account the spatial autocorrelation of tracking rates. To do this, and therefore to make a more stringent test of effects of independent variables, we screened the selected variables in two ways.

First, we added to the initial MAM a factor BLOCK as a fixed effect to represent variation in tracking rate among the 11 survey blocks. Any variables that were not significant after the inclusion of BLOCK were deleted from the model one by one, beginning with the least significant, until all remaining variables were significant.

Secondly, we calculated an autocovariance term *autocov* using the autologistic method of Augustin, Mugglestone & Buckland (1996). We adapted their equation 1 to give a value for *autocov* for the *i*th tracking strip as:

$$autocov_i = \sum_{j \neq i}^{j=n} (y_j / d_{ij}) \Big/ \sum_{j \neq i}^{j=n} (1/d_{ij}) \qquad \text{eqn 1}$$

where $y_j$ is the tracking rate at the *j*th strip and $d_{ij}$ is the distance between the *i*th and *j*th strips. Summation was carried over all $n = 157$ strips except the *i*th strip. Variables in the initial MAM that were no longer significant after the inclusion of *autocov* were deleted as in method 1.

### *Number of large bushes in relation to satellite image data*

Least-squares linear regression was carried out with the number of large bushes in a 10-m square plot as the dependent variable and the reflectance values for the nine Landsat bands and NDVI and their squares as the independent variables. We used GLIM 4 to fit the models and a step-up model selection procedure. *F*-statistics were used to assess the significance of effects.

### *Comparing the performance of models based on different types of data*

We used receiver operating characteristic (ROC) analysis (Metz 1978) to compare the performance of MAM of tracking rates based upon vegetation data, satellite data and densities of large bushes estimated from satellite data. ROC analysis avoids the use of an arbitrary choice of threshold for defining expected presences and absences (Manel, Williams & Ormerod 2001). We calculated the expected number of tracking events at each strip under a particular model and then used various threshold values of this score to generate a plot of sensitivity against (1 – specificity) from each confusion matrix of observed and expected presences and absences. The area under the curve (AUC) was obtained from this plot. The numbers of nights of monitoring per strip were unequal and contributed to the calculation of expected values, so the usual assumption that AUC = 0·5 under the null hypothesis was not correct. We therefore calculated $AUC_{nul}$ under a null model that assumed that the tracking rate was the same for all strips, and calculated a performance score from the AUC for a particular model as:

$$(AUC - AUC_{nul})/(1 - AUC_{nul}) \qquad \text{eqn 2}$$

This score could vary between 0 for a model that performed no better than the null model, to 1 for a model that discriminated perfectly between tracked and untracked strips.

## Results

### OCCURRENCE OF JERDON'S COURSER

Footprints of Jerdon's coursers were recorded on a total of 24 tracking strips in seven of the 11 blocks (Table 1). Except for block H, where the species has been seen repeatedly since its rediscovery in 1986 (Bhushan 1986), these are new localities for Jerdon's courser. While three of the blocks with new records were within 1 km of the previously known site H, the other three (A, B and K) were 15, 7 and 4 km away (Fig. 1) and one lay outside the boundary of the sanctuary. The call of Jerdon's courser (Jeganathan & Wotton 2004) was heard in blocks B, E, F, G and H (P. Jeganathan, unpublished observations), in all of which tracks were also recorded.

### VEGETATION AND GROUND COVER OF SURVEY SITES

The relative abundances of the 12 most common bush and tree species are shown in Fig. 2. Details of plant names are given in Table 2. The dominant woody vegetation in the survey plots was shrubs, particularly *Zizyphus rugosa*, *Carissa carandas* and *Acacia horrida*. The first three components from the PCA of species composition accounted for 50% of the variation among plots (23%, 15% and 12%, respectively; eigenvalues 2·76, 1·80, 1·44). PC1 was positively associated with the relative abundance of *Tarenna asiatica*, *Diospyros ferrea* and *Pleiospermium alatum* and negatively associated with *Zizyphus rugosa*. PC2 was positively associated with the relative abundance of *Randia dumetorum* and *Grewia rhamnifolia* and negatively associated with *Carissa carandas* and *Maytenus emarginata*. PC3 was positively associated with the relative abundance of *Zizyphus rugosa* and negatively associated with *Acacia horrida* and *Canthium parviflorum* (Table 2). Correlations

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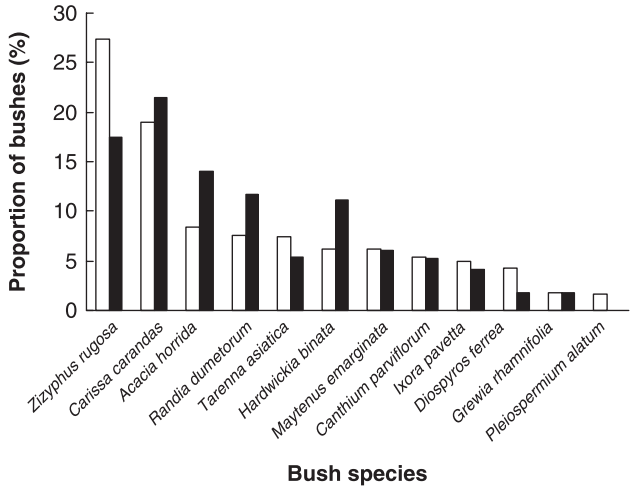


**Fig. 2.** Mean percentage composition of trees and bushes in 10-m square vegetation survey plots that contained tracking strips from which tracks of Jerdon's courser were (filled bars) or were not (open bars) recorded. Species are presented from left to right in order of descending overall abundance.

**Table 1.** Deployment of tracking strips and records of tracks of Jerdon's courser in the 11 blocks shown in Fig. 1

| Block | First strip deployed | Last check | Number of strips | Strip nights | Jerdon's courser tracking events | Strips with Jerdon's courser tracks |
|---|---|---|---|---|---|---|
| A | 15 Feb 2002 | 6 Mar 2002 | 14 | 231 | 3 | 3 |
| B | 9 Dec 2001 | 18 Feb 2002 | 17 | 435 | 3 | 2 |
| C | 6 Dec 2001 | 21 Feb 2002 | 12 | 477 | 0 | 0 |
| D | 19 Feb 2002 | 28 Mar 2002 | 16 | 555 | 0 | 0 |
| E | 11 Apr 2002 | 3 May 2002 | 12 | 247 | 1 | 1 |
| F | 8 Apr 2002 | 24 May 2002 | 15 | 756 | 1 | 1 |
| G | 8 Apr 2002 | 25 May 2002 | 11 | 334 | 4 | 4 |
| H | 30 Jan 2001 | 13 Jun 2002 | 18 | 863 | 27 | 11 |
| I | 25 Apr 2001 | 6 Jun 2001 | 16 | 421 | 0 | 0 |
| J | 8 Dec 2001 | 21 Feb 2002 | 10 | 313 | 0 | 0 |
| K | 8 Dec 2001 | 20 Feb 2002 | 16 | 477 | 3 | 2 |
| Total | | | 157 | 5109 | 42 | 24 |

**Table 2.** Correlations of species' abundances with the first three principal components from an analysis of the proportions of the 12 most abundant tree and bush species in the study areas. Proportions were arcsine square root transformed before analysis

| Species | PC1 | PC2 | PC3 |
|---|---|---|---|
| *Zizyphus rugosa* Lam. | −0·561 | 0·269 | 0·672 |
| *Carissa carandas* L. | −0·268 | −0·687 | −0·061 |
| *Acacia horrida* Span. | −0·100 | −0·445 | −0·563 |
| *Randia dumetorum* Lam. | −0·082 | 0·532 | −0·377 |
| *Tarenna asiatica* (L.) Kuntze | 0·771 | 0·085 | 0·077 |
| *Hardwickia binata* Roxb. | −0·009 | 0·228 | −0·242 |
| *Maytenus emarginata* (Willd.) Ding Hou | 0·289 | −0·561 | 0·266 |
| *Canthium parviflorum* Bartl. Ex DC | 0·317 | −0·072 | −0·507 |
| *Ixora pavetta* Roxb. | 0·547 | −0·103 | 0·311 |
| *Diospyros ferrea* (Willd.) Bakh. | 0·819 | 0·147 | 0·057 |
| *Grewia rhamnifolia* Roth | −0·269 | 0·595 | −0·167 |
| *Pleiospermium alatum* Swingle | 0·732 | 0·250 | 0·047 |

among the relative abundances of these species are given in Appendix 1.

Most bushes were < 2 m tall (Table 3) and *Hardwickia binata* was the only common species that often exceeded 4 m in height. Mean values of the principal components scores varied considerably among blocks. Evidence of cutting of trees and bushes by humans was visible in > 60% of survey plots in all blocks. Grasses covered about half of the ground surface. The main substrate types were stones (*c.* 40%) and fine soil (*c.* 60%).

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**Table 3.** Means and standard errors (italics) in survey blocks for counts of bushes, *Cymbopogon citratus* grass tussocks and *Dodonaea viscosa* plants, percentage cover of substrate types and other grasses, proportion of plots in which there was evidence of wood cutting (Cut) and the first three principal components from an analysis of the species composition of trees and bushes. Means for all plots containing strips with and without Jerdon's courser (JC) records are also shown. Sample sizes are given in Table 1

| Block | Small bush | | Large bush | | *Cymbopogon* | | *Dodonaea* | | Stones | | Gravel | | Soil | | Grass | | Cut | | PC1 | | PC2 | | PC3 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| A | 25·4 | *2·3* | 4·1 | *0·9* | 0 | *0* | 1·4 | *0·4* | 80 | *5* | 0 | *0* | 20 | *5* | 61 | *4* | 0·93 | | −0·80 | *0·09* | −0·40 | *0·17* | 1·08 | *0·19* |
| B | 24·6 | *2·7* | 4·5 | *0·8* | 0 | *0* | 6·0 | *1·0* | 95 | *9* | 0 | *0* | 41 | *9* | 64 | *3* | 0·94 | | −0·32 | *0·13* | −0·86 | *0·12* | 0·34 | *0·23* |
| C | 20·8 | *3·6* | 4·9 | *1·2* | 0 | *0* | 6·3 | *1·6* | 20 | *7* | 8 | *8* | 71 | *10* | 69 | *7* | 0·83 | | 0·28 | *0·21* | −0·60 | *0·25* | −0·19 | *0·23* |
| D | 47·6 | *4·6* | 10·8 | *1·6* | 0 | *0* | 2·4 | *0·6* | 19 | *6* | 0 | *0* | 81 | *6* | 57 | *4* | 1·00 | | 1·52 | *0·28* | 0·49 | *0·23* | 0·05 | *0·17* |
| E | 39·8 | *8·3* | 10·4 | *2·6* | 0 | *0* | 10·1 | *1·8* | 46 | *11* | 0 | *0* | 54 | *11* | 56 | *3* | 1·00 | | 0·20 | *0·34* | 0·43 | *0·20* | −0·10 | *0·18* |
| F | 36·3 | *3·2* | 8·8 | *2·3* | 0 | *0* | 16·1 | *1·6* | 30 | *10* | 18 | *8* | 53 | *10* | 38 | *4* | 0·87 | | 0·37 | *0·24* | −0·18 | *0·24* | 0·72 | *0·21* |
| G | 33·7 | *7·9* | 4·8 | *1·4* | 0 | *0* | 13·8 | *2·7* | 33 | *13* | 9 | *9* | 58 | *14* | 37 | *8* | 1·00 | | 0·45 | *0·20* | 0·05 | *0·24* | −0·25 | *0·31* |
| H | 19·0 | *3·0* | 3·4 | *0·9* | 0 | *0* | 11·1 | *1·5* | 13 | *4* | 6 | *6* | 81 | *7* | 64 | *4* | 0·61 | | −0·18 | *0·14* | −0·60 | *0·21* | −1·01 | *0·18* |
| I | 21·3 | *2·2* | 3·4 | *0·6* | 0 | *0* | 8·8 | *1·2* | 31 | *6* | 0 | *0* | 69 | *6* | 63 | *5* | 0·75 | | 0·10 | *0·20* | 0·02 | *0·13* | −0·48 | *0·26* |
| J | 20·8 | *2·7* | 6·4 | *1·4* | 0·1 | *0·1* | 17·1 | *2·7* | 61 | *12* | 6 | *6* | 34 | *12* | 72 | *5* | 0·80 | | −0·70 | *0·16* | −0·05 | *0·15* | 0·60 | *0·19* |
| K | 48·0 | *6·3* | 8·2 | *1·1* | 16·4 | *2·5* | 0·4 | *0·4* | 65 | *7* | 4 | *4* | 31 | *7* | 64 | *6* | 1·00 | | −0·96 | *0·08* | 1·71 | *0·13* | −0·38 | *0·24* |
| No JC | 32·6 | *1·8* | 6·7 | *0·5* | 1·6 | *0·5* | 7·9 | *0·7* | 42 | *3* | 4 | *2* | 54 | *3* | 60 | *2* | 0·89 | | 0·04 | *0·09* | 0·02 | *0·09* | 0·10 | *0·08* |
| JC | 21·7 | 1·9 | 3·9 | 0·6 | 2·0 | 1·4 | 9·1 | 1·4 | 34 | 7 | 5 | 4 | 62 | 8 | 55 | 5 | 0·83 | | −0·22 | 0·15 | −0·12 | 0·18 | −0·56 | 0·22 |

### TRACKING RATE IN RELATION TO VEGETATION AND SUBSTRATE

Logistic regression analysis was carried out in which the probability per strip night of a Jerdon's courser tracking event was modelled in relation to all of the variables listed in Table 3. When data from all strips were included and spatial autocorrelation was not considered, the selected MAM included a negative effect on tracking rate of the density of small bushes, a quadratic effect of the density of large bushes, with an optimum at 5·59 bushes 10-m square plot (559 bushes ha$^{-1}$) and a negative effect of PC3 score (Table 4). Strips tracked by Jerdon's coursers tended to have low densities of small and large bushes and PC3 scores below the overall median (Fig. 3). There was a unimodal relationship between tracking rate and the density of large bushes (Fig. 4). Comparison of mean percentage composition of common bush species in plots where the strip was or was not tracked by Jerdon's courser indicated a lower relative abundance of *Zizyphus rugosa* at tracked than untracked sites and higher abundances of *Acacia horrida*, *Randia dumetorum* and *Hardwickia binata* (Fig. 2). These differences were in accord with the correlations of these species with the PC3 score (Table 2) and the negative effect of the PC3 score on tracking rate.

When the four blocks in which Jerdon's courser tracks were not found were excluded from the analysis, the MAM included the same variables and the model parameter estimates were similar (Table 4). There was significant variation in tracking rate among blocks when the factor BLOCK was added to the MAM selected for data from all blocks. The effect of the spatial autocorrelation variable *autocov* was also highly significant. When BLOCK or *autocov* were included in the model the effect of PC3 score became non-significant. When BLOCK was included in the model the effect of the density of small bushes became non-significant, but it remained significant when *autocov* was included. The quadratic effect of large bush density remained significant in this model and the optimum bush density also remained similar.

### TRACKING RATE IN RELATION TO SATELLITE IMAGE DATA

Jerdon's courser tracking rate was modelled as a function of reflectance values in all bands and the derived variable NDVI by logistic regression. When data from all strips were included and spatial autocorrelation was not considered, the selected MAM included a positive effect of band 6·2 reflectance, a quadratic effect of band 7 reflectance, with an optimum at 61·5 units and a negative effect of band 8 reflectance (Table 5). This last effect only just attained statistical significance ($P$ = 0·05). Tracked strips had high band 6·2 reflectance and intermediate band 7 reflectance (Fig. 5).

When the four blocks in which Jerdon's courser tracks were not recorded were excluded from the analysis, the

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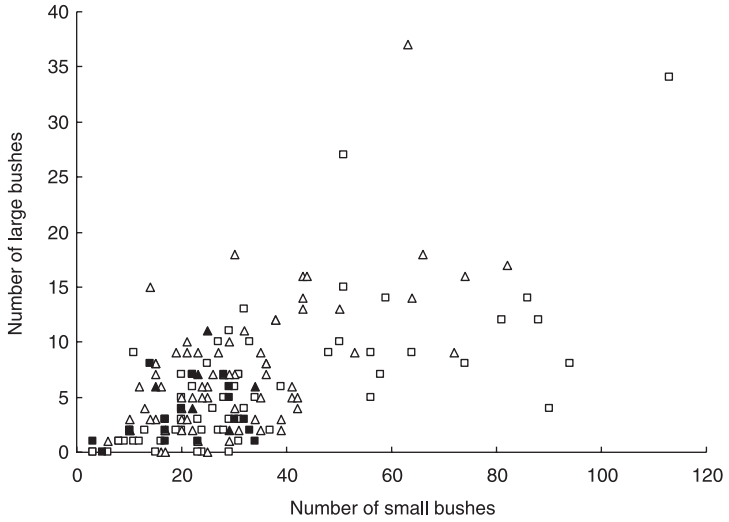


**Fig. 3.** Numbers of large (> 2 m high) and small (< 2 m) bushes in 10-m square vegetation survey plots centred on 157 tracking strips. Each point represents a plot. Filled symbols denote plots that contained strips from which tracks of Jerdon's courser were recorded, and open symbols strips where they were not recorded. Squares represent plots with scores of the third principal component of vegetation composition (PC3) below the median, and triangles represent plots with PC3 scores at or above the median.

**Table 4.** Minimal adequate logistic regression models relating the logit of the probability of a Jerdon's courser (JC) tracking event occurring per strip night of monitoring to vegetation and substrate variables measured in a 10-m square plot centred on the strip. Variables listed in Table 2 that do not appear in this table did not have a significant effect at $P < 0{\cdot}05$. Significance levels from likelihood-ratio tests for deletion of variables from the final model are shown by asterisks, $*P < 0{\cdot}05$, $**P < 0{\cdot}01$, $***P < 0{\cdot}001$. The significance level given for the main effect of large bushes is that for the main effect and quadratic term combined. The significance levels for the constant term in the two right-hand columns refer to the effects of block as a factor and the spatial autocorrelation term, respectively

| Model specification and variables | Parameter estimates | | | |
|---|---|---|---|---|
| Blocks without JC excluded? | No | Yes | No | No |
| Block effect included in model? | No | No | Yes | No |
| Autologistic effect included in model? | No | No | No | Yes |
| Constant | −5·346 | −4·843 | *** | *** |
| Small bushes | −0·03947** | −0·04611*** | NS | −0·03256* |
| Large bushes | +0·7060*** | +0·7897*** | +0·6908*** | +0·5493** |
| (Large bushes)$^2$ | −0·06138*** | −0·07062*** | −0·06772*** | −0·04966** |
| PC3 | −0·5791*** | −0·4883** | NS | NS |
| Residual deviance | 109·47 | 72·81 | 60·84 | 86·63 |
| Residual d.f. | 152 | 103 | 144 | 152 |

effect of band 8 reflectance was no longer significant (Table 5). There was significant variation in tracking rate among blocks when the factor BLOCK was added to the MAM selected for data from all blocks. The effect of the spatial autocorrelation variable *autocov* was also significant. When BLOCK or *autocov* were included in the model the effects of band 6·2 and band 8 reflectances both became non-significant. However, the quadratic effect of band 7 reflectance remained highly significant and the optimum band 7 reflectance value also remained similar. There were strong correlations between reflectance values for some bands (see Appendix 2) so models incorporating different sets of bands would be expected to perform almost as well as the MAM.

### DENSITY OF LARGE BUSHES IN RELATION TO SATELLITE IMAGE DATA

The effect of the density of large bushes on tracking rate was highly significant and robust under different formulations of the model. Accordingly, we carried out a two-step analysis in which we first modelled the density of large bushes using satellite data and then related tracking rate to estimated large bush density. This approach was considered to be potentially valuable in facilitating the mapping of suitable habitats for Jerdon's courser in other areas (see the Discussion).

Regression analysis of the number of large bushes on reflectance values for all Landsat bands and the derived variable NDVI identified a MAM that included

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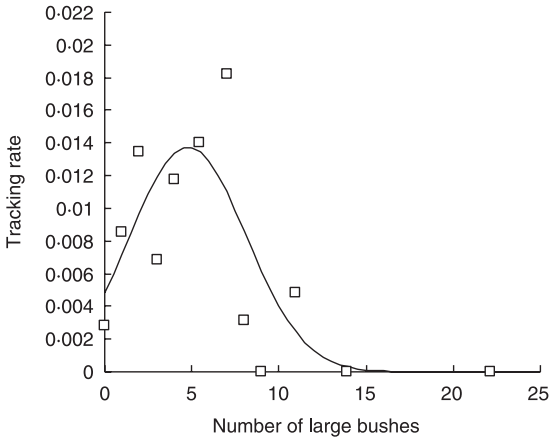


**Fig. 4.** Number of Jerdon's courser tracking events per strip night in relation to the number of large (> 2 m high) bushes in a 10-m$^2$ plot centred on the tracking strip. Plotted points are for groups of bush number categories, which were grouped so that no category contained data for less than 300 strip nights. The curve is from the MAM (see text).

negative effects of band 5 and band 8 reflectances. The fitted model was:

number of large bushes per plot = 47·78 – 0·1689 × band 5 – 0·5166 × band 8.

Both effects were significant at $P < 0{\cdot}01$. The correlation between the observed and estimated numbers of large bushes was $r = 0{\cdot}525$. A plot of mean band 8 against band 5 values for groups of survey plots with the same or similar numbers of large bushes showed that reflectances in band 5 and band 8 tended to be lower where there were many large bushes (Fig. 6).

### TRACKING RATE IN RELATION TO THE DENSITY OF LARGE BUSHES ESTIMATED FROM SATELLITE IMAGE DATA

Logistic regression analysis was carried out of tracking rate in relation to the estimated number of large bushes

**Table 5.** Minimal adequate logistic regression models relating the logit of the probability of a Jerdon's courser (JC) tracking event occurring per strip night of monitoring to Landsat data for the pixel in which the strip lay. Landsat bands that do not appear in this table did not have a significant effect at $P < 0{\cdot}05$. Significance levels from likelihood-ratio tests for deletion of variables from the final model are shown by asterisks, *$P < 0{\cdot}05$, **$P < 0{\cdot}01$, ***$P < 0{\cdot}001$. The significance level given for the main effect of band 7 is that for the main effect and quadratic term combined. The significance levels for the constant term in the two right-hand columns refer to the effects of block as a factor and the spatial autocorrelation term, respectively

| Model specification and variables | Parameter estimates | | | |
|---|---|---|---|---|
| Blocks without JC excluded? | No | Yes | No | No |
| Block effect included in model? | No | No | Yes | No |
| Autologistic effect included in model? | No | No | No | Yes |
| Constant | −142·8 | −113·0 | *** | *** |
| Band 6·2 | +0·4881*** | +0·3465** | NS | NS |
| Band 7 | +2·226*** | +1·767*** | +1·416*** | +1·744*** |
| (Band 7)$^2$ | −0·01811*** | −0·01464*** | −0·01179*** | −0·01399*** |
| Band 8 | −0·1663* | NS | NS | NS |
| Residual deviance | 94·66 | 84·43 | 64·43 | 87·84 |
| Residual d.f. | 152 | 99 | 144 | 153 |

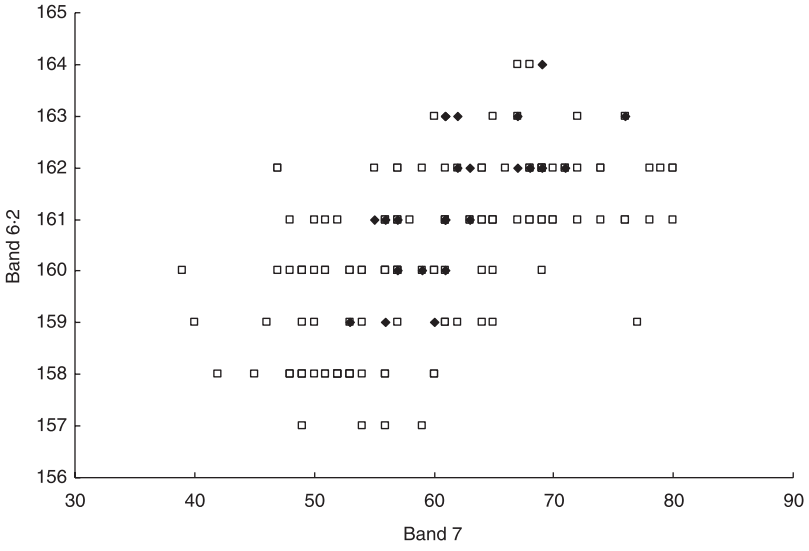


**Fig. 5.** Landsat 7 reflectance in band 6·2 in relation to that in band 7 for pixels containing tracking strips on which Jerdon's courser footprints were recorded (filled diamonds) and were not recorded (open squares).

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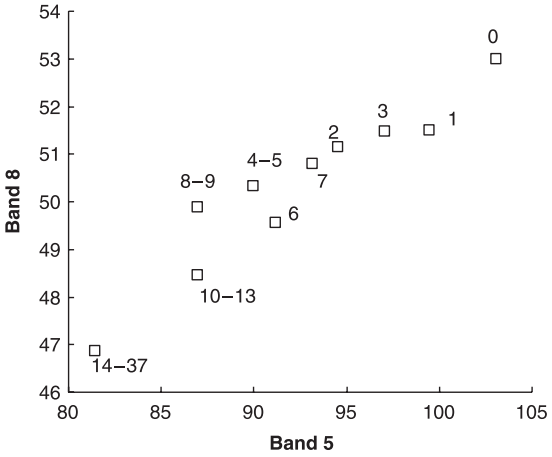


**Fig. 6.** Mean Landsat band 5 and band 8 reflectance values for pixels containing 10-m square vegetation survey plots with different numbers of large bushes. Each point represents the mean for all plots, with the number of bushes identified by the number or range of numbers next to the data point. Bush number categories were grouped so that each group contained data from at least 10 plots.

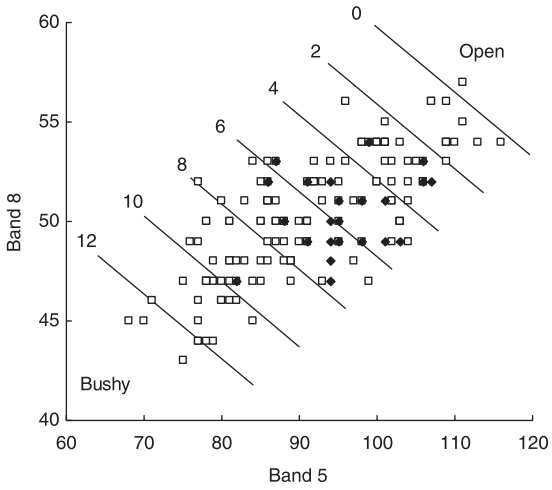


**Fig. 7.** Landsat 7 reflectance in band 8 in relation to that in band 5 for pixels containing tracking strips on which Jerdon's courser footprints were recorded (filled diamonds) and were not recorded (open squares). Lines show isopleths for the number of large bushes expected from a regression model of large bush number per $10 \times 10$-m plot in relation to band 5 and band 8 reflectance. Lines are labelled according to the expected number of large bushes.

per 10-m square plot, obtained from satellite data as described in the previous section. One slightly negative value for the estimated number of large bushes (–0·4) was altered to 0 before the analysis. When data from all strips were included and the effect of spatial autocorrelation was not considered, the quadratic effect of the estimated density of large bushes was highly significant (Table 6). The optimum was 5·57 bushes per 10-m square plot (557 bushes $ha^{-1}$). Strips that were tracked by Jerdon's courser tended to lie in pixels that had intermediate reflectances in bands 5 and 8, and intermediate expected numbers of large bushes (Fig. 7). There was a unimodal relationship between tracking rate and estimated large bush density (Fig. 8). When the four blocks in which Jerdon's courser tracks were not found were excluded from the analysis, the quadratic effect of estimated density of large bushes remained significant. There was significant variation in tracking rate among blocks when the factor BLOCK was added to the MAM selected for data from all blocks. The effect of the spatial auto-correlation variable *autocov* was also significant. When either BLOCK or *autocov* was included in the model the quadratic effect of estimated large bush density remained significant (Table 6) and the optimum large bush density remained similar.

## Discussion

### HABITAT PREFERENCES OF JERDON'S COURSER

Our most robust finding was that Jerdon's coursers were most likely to occur in areas of scrub jungle with intermediate densities of large bushes. All the MAM based upon vegetation survey data supported this conclusion, as did the models based upon satellite imagery, because they showed a consistent quadratic effect of band 7 reflectance. There was a significant correlation between the density of large bushes and band 7 reflectance ($r = -0{\cdot}462$; $P < 0{\cdot}001$). The fact that band 5 and

**Table 6.** Minimal adequate logistic regression models relating the logit of the probability of a Jerdon's courser (JC) tracking event occurring per strip night of monitoring to the number of large bushes per 10-m square estimated from Landsat bands 5 and 8 for the pixel in which the strip lay. Significance levels from likelihood-ratio tests for deletion of variables from the final model are shown by asterisks, $*P < 0{\cdot}05$, $**P < 0{\cdot}01$, $***P < 0{\cdot}001$. The significance level given for the main effect of estimated large bush number is that for the main effect and quadratic term combined. The significance levels for the constant term in the two right-hand columns refer to the effects of block as a factor and the spatial autocorrelation term, respectively

| Model specification and variables | Parameter estimates | | | |
|---|---|---|---|---|
| Blocks without JC excluded? | No | Yes | No | No |
| Block effect included in model? | No | No | Yes | No |
| Autologistic effect included in model? | No | No | No | Yes |
| Constant | −10·89 | −10·21 | *** | *** |
| Estimated large bushes | +2·490*** | +2·259*** | +1·868*** | +1·860*** |
| (Estimated large bushes)$^2$ | −0·2235*** | −0.1978*** | −0·1513*** | −0·1617*** |
| Residual deviance | 110·14 | 90·04 | 62·80 | 86·51 |
| Residual d.f. | 154 | 100 | 144 | 153 |

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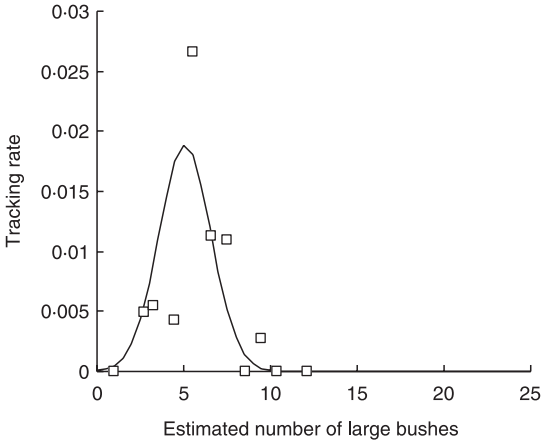


**Fig. 8.** Number of Jerdon's courser tracking events per strip night in relation to the number of large (> 2 m high) bushes in the area around each strip estimated from Landsat band 5 and band 8 reflectances (see text). Plotted points are for groups of bush number categories, which were grouped so that no category contained data for less than 300 strip nights. The curve is from the MAM (see text).

8 reflectances, rather than band 7 reflectance, were selected as the best correlates of bush density is a result of high correlations among the reflectances for bands 5, 7 and 8 (see Appendix 2). Hence, the vegetation- and satellite imagery-based models both support a strong effect of the density of large bushes. Densities of about 300–700 large (> 2 m tall) bushes $ha^{-1}$ and less than 1000 small (< 2 m) bushes $ha^{-1}$ are likely to be favourable to Jerdon's coursers. Less quantitative descriptions of Jerdon's courser habitat (summarized in BirdLife International 2001) are in accord with this finding. Descriptions of the habitat preferences of the two African congeners of Jerdon's courser, *Rhinoptilus cinctus* (Heuglin) and, particularly, *Rhinoptilus chalcopterus* (Temminck), also emphasize the importance of lightly wooded habitats and scrub (Maclean 1996). This genus is unusual among nocturnal, visually foraging, charadriiform birds in using wooded areas where average light levels are likely to be low at night because of the shading effect of the canopy (Martin 1990). However, our results suggest that coursers may still be able to see invertebrate prey on the ground by selecting relatively well-illuminated open areas.

These results suggest that land use by humans and grazing and browsing by wild and particularly domestic large herbivores have important effects on the suitability of habitat for Jerdon's courser. The effects of domestic livestock on vegetation far outweigh those of wild gazelles and deer, as evidenced by the frequency of tracks on tracking strips (P. Jeganathan, unpublished observations). Mechanical clearing of bushes to create pasture, orchards or tilled land, high levels of woodcutting and too high a level of use by domestic livestock are likely to create habitats with too few bushes for Jerdon's coursers. However, a low level of grazing and browsing by livestock or an absence of woodcutting might well lead to numbers of bushes that are too high. Tracking strips were crossed frequently by domestic water buffalo, sheep and goats, and evidence of woodcutting was apparent in all of our survey blocks, so the level of use of the reserve and adjacent areas by humans is clearly a relevant issue for conservation managers. Quantitative monitoring, together with a study of the social and economic factors that affect land use, would assist the management of the reserve.

### VALUE OF TRACKING DATA FOR THE STUDY OF HABITAT SELECTION

The monitoring of tracking strips has several advantages as a method for studying habitat selection by the secretive and nocturnally active Jerdon's courser. Visual records of Jerdon's courser are difficult to obtain and require time-consuming searches by night. Conclusions about habitat selection from night searches are likely to be biased because the ease with which birds are detected is probably greatest in areas with few bushes and sparse ground vegetation. Tracking has the potential disadvantage that the tracks of other bird species, most probably yellow-wattled lapwing *Vanellus malarbaricus* Boddaert and chestnut-bellied sandgrouse *Pterocles exustus* Temminck, might be mistaken for those of Jerdon's courser. However, confusion with lapwing footprints is unlikely in this study because the overlap in footprint characteristics between the two species is small (Jeganathan *et al*. 2002) and yellow-wattled lapwings are rarely seen in the types of habitat included in our survey. None was seen in our study blocks, even though lapwings are diurnal and easy to see in their preferred, more open habitats. Chestnut-bellied sandgrouse were often seen in the study areas, but close examination of footprints of this species allows accurate identification (Jeganathan *et al*. 2002; P. Jeganathan & R.E. Green, unpublished data). Diagnostic characters include the size of pad at the junction of the toes (larger in sandgrouse), a different position of the junction of toes with the pad and distinctive drag marks from the claw of the central toe of the sandgrouse.

### RELATIVE MERITS OF GROUND-BASED VEGETATION SURVEY DATA AND SATELLITE IMAGERY IN MODELLING JERDON'S COURSER HABITAT SELECTION

The logistic regression analysis of Jerdon's courser tracking rates on ground-based vegetation survey data and satellite imagery both yielded statistical models that included highly significant effects. The performance of the two approaches can be compared directly because they both started with similar numbers of candidate variables. We compared the performance of the MAM derived from the two approaches in discriminating sites where Jerdon's courser tracks were recorded from those where they were not by using ROC analysis (see the Statistical analysis). The performance scores from models based on satellite imagery directly and on

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**Table 7.** Performance of minimal adequate logistic regression models of tracking rate in relation to vegetation survey data, satellite imagery and densities of large bushes estimated from satellite imagery in discriminating 24 strips tracked by Jerdon's courser from 133 that were not tracked. For models using satellite data and expected numbers of large bushes the inclusion of block effects or a spatial autocorrelation (SA) term both led to the final models with the same independent variables. The performance measure is derived from the AUC of an ROC plot (see the Methods). In each case, the performance of models fitted with and without excluding the blocks in which Jerdon's courser (JC) tracks were not recorded is evaluated on the whole data set

| Data used for model | Blocks without JC excluded? | Spatial autocorrelation term/block effect? | Number of fitted parameters in the model | $(AUC - AUC_{nul})/(1 - AUC_{nul})$ |
|---|---|---|---|---|
| Vegetation survey | No | No | 5 | 0·324 |
| Vegetation survey | Yes | No | 5 | 0·317 |
| Vegetation survey | No | Yes (block) | 3 | 0·151 |
| Vegetation survey | No | Yes (SA) | 4 | 0·167 |
| Satellite imagery | No | No | 5 | 0·411 |
| Satellite imagery | Yes | No | 4 | 0·395 |
| Satellite imagery | No | Yes | 3 | 0·333 |
| Large bushes estimated from satellite | No | No | 3 | 0·395 |
| Large bushes estimated from satellite | Yes | No | 3 | 0·389 |
| Large bushes estimated from satellite | No | Yes | 3 | 0·395 |

densities of large bushes estimated from satellite data were higher than for models based on ground surveys of vegetation, even though the MAM based on vegetation data required more fitted parameters (Table 7). This may be because the satellite-based methods measured habitat characteristics over a larger area (14–57 m square) around each tracking strip than the ground survey (10-m square). We chose a small plot size for the ground survey because of fieldwork time constraints, but range use by Jerdon's coursers might be affected by habitat characteristics over a larger area.

We consider that models based upon ground-based vegetation survey data and satellite imagery are complementary in their potential applications. Ground-based vegetation survey analyses yield conclusions about effects of detailed habitat characteristics directly relevant to habitat management decisions. Analyses based upon satellite imagery alone, without extensive ground truth surveys, would be unlikely to yield results with such direct relevance. The value of the satellite-based approaches lies in their potential application to the mapping of suitable habitat over large areas.

### USE OF SATELLITE IMAGERY TO IDENTIFY PRIORITY AREAS FOR JERDON'S COURSER SURVEYS

The use of models that relate the distribution or abundance of an animal to environmental variables is a potentially valuable approach to mapping the probable distribution of species that are difficult to survey (Fielding & Bell 1997; Rushton 2004). One approach is to fit species-reflectance models in which distribution or abundance is related directly to reflectance values from satellite imagery (Avery & Haines-Young 1990). An alternative approach is to first make a habitat-reflectance model and then use knowledge of species–habitat relationships to infer the distribution pattern from a map of suitable habitats. We call this the two-step procedure. As vegetation cover often has important effects on the suitability of an area for a species, measurements of vegetation type and extent from remote sensing have frequently been employed for deriving habitat information as an input variable for distribution modelling (Osborne, Alonso & Bryant 2001; Saveraid *et al*. 2001; Gibson *et al.*).

A limitation with both modelling approaches is the difficulty of using models fitted using remote sensing data from one image to generate inferred species' distributions from another image. Differences between images in the season in which the image was obtained, atmospheric conditions and soil moisture may adversely affect the reliability of extrapolation of a model to another image. This problem is especially severe for species-reflectance models, which tend not to work well when applied to areas other than the ones in which they were developed (Nagendra 2001). Carrying out ground-based species surveys to recalibrate the model for a new image is likely to be expensive and may be impossible if the species is scarce or absent in the new area. Although a similar problem arises for the two-step approach, the consequences are less severe because calibration studies involving ground-based surveys of habitat are usually easier and cheaper to conduct than surveys of species distribution or abundance.

Other factors can limit the usefulness of both modelling approaches. The focal species may respond to variables that remote sensing does not measure effectively, such as the presence of a rare food plant or the three-dimensional architecture of vegetation. Although technical advances may allow the measurement of some of these, such as vegetation architecture (Hinsley *et al*. 2002; Lefsky *et al*. 2002), there will often be components of a species' habitat requirements that are insufficiently known or beyond the scope of current remote sensing technology. Inferences about distribution or abundance from models with such deficiencies are likely to be unreliable. Even if a model appears to

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perform well in one area, this may be because variables that really influence the distribution and abundance, but are not measured by remote sensing data, are closely correlated with other variables that are measured. If this correlation is weaker in other areas then the model's performance will be diminished. Such problems are difficult to guard against, but the two-step approach has the advantage that knowledge of the species' ecological requirements from autecological studies of ranging behaviour or diet can help to identify relationships that are likely to represent causation rather than just correlation.

Bearing these caveats in mind, we consider that the two-step approach can be applied successfully to the problem of surveying the potential distribution of Jerdon's courser. It would be relatively easily to overcome differences between images due to factors such as atmospheric conditions by recalibrating the relationship between the density of large bushes and satellite data by new ground surveys of bush density. Bush densities could then be estimated from the new image and areas suitable for Jerdon's courser could be mapped. Although much scrub jungle within the historical range of Jerdon's courser has been cleared, substantial areas remain. Given the difficulty in detecting the Jerdon's courser, it seems likely that unknown populations exist in other areas. Finding these populations is important because of possible threats from habitat clearance. Mapping of potential habitat using satellite imagery and the models developed here would enable suitable areas to be identified and surveyed on the ground to detect the species. Given the restricted known range of this critically endangered species, we suggest that surveys based upon these principles should have high priority.

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## Appendix 1

Pearson correlation coefficients between arcsine square root-transformed proportions of the 12 most abundant bush species in the 157 vegetation survey plots

| Species | *Zr* | *Cc* | *Ah* | *Rd* | *Ta* | *Hb* | *Me* | *Cp* | *Ip* | *Df* | *Gr* |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Zizyphus rugosa* (*Zr*) | | | | | | | | | | | |
| *Carissa carandas* (*Cc*) | −0·120 | | | | | | | | | | |
| *Acacia horrida* (*Ah*) | −0·341 | 0·131 | | | | | | | | | |
| *Randia dumetorum* (*Rd*) | −0·077 | −0·205 | −0·047 | | | | | | | | |
| *Tarenna asiatica* (*Ta*) | −0·314 | −0·225 | −0·105 | −0·007 | | | | | | | |
| *Hardwickia binata* (*Hb*) | −0·309 | −0·237 | −0·169 | 0·008 | −0·108 | | | | | | |
| *Maytenus emarginata* (*Me*) | −0·178 | 0·159 | 0·057 | −0·224 | 0·169 | −0·145 | | | | | |
| *Canthium parviflorum* (*Cp*) | −0·377 | −0·003 | 0·053 | −0·003 | 0·133 | −0·129 | −0·042 | | | | |
| *Ixora pavetta* (*Ip*) | −0·215 | −0·139 | −0·153 | −0·123 | 0·273 | −0·091 | 0·232 | 0·047 | | | |
| *Diospyros ferrea* (*Df*) | −0·374 | −0·230 | −0·188 | −0·007 | 0·566 | −0·007 | 0·180 | 0·149 | 0·294 | | |
| *Grewia rhamnifolia* (*Gr*) | 0·169 | −0·222 | −0·087 | 0·306 | −0·151 | −0·056 | −0·261 | 0·003 | −0·180 | −0·106 | |
| *Pleiospermium alatum* | −0·245 | −0·289 | −0·102 | −0·029 | 0·496 | −0·085 | −0·032 | 0·153 | 0·268 | 0·579 | −0·062 |

## Appendix 2

Pearson correlation coefficients among Landsat band reflectance values and NDVI scores in 157 pixels containing tracking strips and centres of vegetation survey plots

| | NDVI | Band 1 | Band 2 | Band 3 | Band 4 | Band 5 | Band 7 | Band 6·1 | Band 6·2 |
|---|---|---|---|---|---|---|---|---|---|
| NDVI | | | | | | | | | |
| Band 1 | −0·679 | | | | | | | | |
| Band 2 | −0·777 | 0·807 | | | | | | | |
| Band 3 | −0·914 | 0·714 | 0·878 | | | | | | |
| Band 4 | −0·087 | 0·284 | 0·470 | 0·472 | | | | | |
| Band 5 | −0·729 | 0·697 | 0·836 | 0·858 | 0·528 | | | | |
| Band 7 | −0·790 | 0·683 | 0·834 | 0·891 | 0·466 | 0·969 | | | |
| Band 6·1 | −0·509 | 0·408 | 0·578 | 0·596 | 0·387 | 0·617 | 0·583 | | |
| Band 6·2 | −0·530 | 0·429 | 0·564 | 0·604 | 0·370 | 0·634 | 0·595 | 0·873 | |
| Band 8 | −0·604 | 0·551 | 0·711 | 0·777 | 0·606 | 0·717 | 0·715 | 0·472 | 0·477 |

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